

A REDESCRIPTION OF *ODILIA EMANUELAE* (NEMATODA: TRICHOSTRONGYLINA: HELIGMONELLIDAE) FROM AUSTRALIAN RODENTS WITH A KEY AND COMMENTS ON THE GENUS *ODILIA*

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Summary

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Odilia emanuelae (Mawson, 1961) is redescribed from a new host, *Rattus leucopus* from Queensland Australia. A key to the genus *Odilia*, based on the number and size of the ridges of the synlophe is given. The relationships of species of the genus *Odilia* with their murid hosts, coevolution or host switching, are discussed and speculation as to the significance of their known biogeographic distribution is put forward.

KEY WORDS: Nematoda, Heligmonellidae, murid, *Rattus*, Australia, phylogeny, biogeography.

Introduction

During a study of the helminth parasites of the Cape York rat, *Rattus leucopus* (Gray), specimens of three species of trichostrongyloid nematodes, Heligmonellidae, were encountered in the duodenum of several hosts. They included *Nippostrongylus brasiliensis* (Travassos, 1914), a cosmopolitan species and *N. magnus* (Mawson, 1961), endemic to Australian rodents. Previously noted from *Rattus fuscipes* (Waterhouse), *R. sordidus* (Gould) and *Melomys cervinipes* (Gould) (see Smales, 1997), *N. magnus* was redescribed by Beveridge & Durette-Desset (1992) from *R. fuscipes* and experimentally infected *Rattus norvegicus* (Berkenhout). The third species found was *Odilia emanuelae* (Mawson, 1961). *Odilia emanuelae* was described originally from *R. sordidus* as *R. conatus* and *R. fuscipes* as *R. assimilis* by Mawson (1961) but she did not describe some features including the cuticular ridges of the synlophe. Subsequently a brief description of the synlophe was given by Durette-Desset (1969) on the basis of one specimen. The additional material from a new host allows a more detailed description to be prepared and a key to known species of the genus given.

The genus *Odilia* has been reported from 11 endemic species of murids from Australia: in the subfamilies Hydromyinae, *Mastacomys fuscus* Thomas, *Melomys burtoni* (Ramsay), *Melomys cervinipes*, *Mesembryomys gouldii* (Gray), *Pseudomys higginsii* (Trouessart), *Uromys caudimaculatus* (Kreffl), *Zyzomys argurus* (Thomas) and *Zyzomys woodwardi* (Thomas); and Murinae,

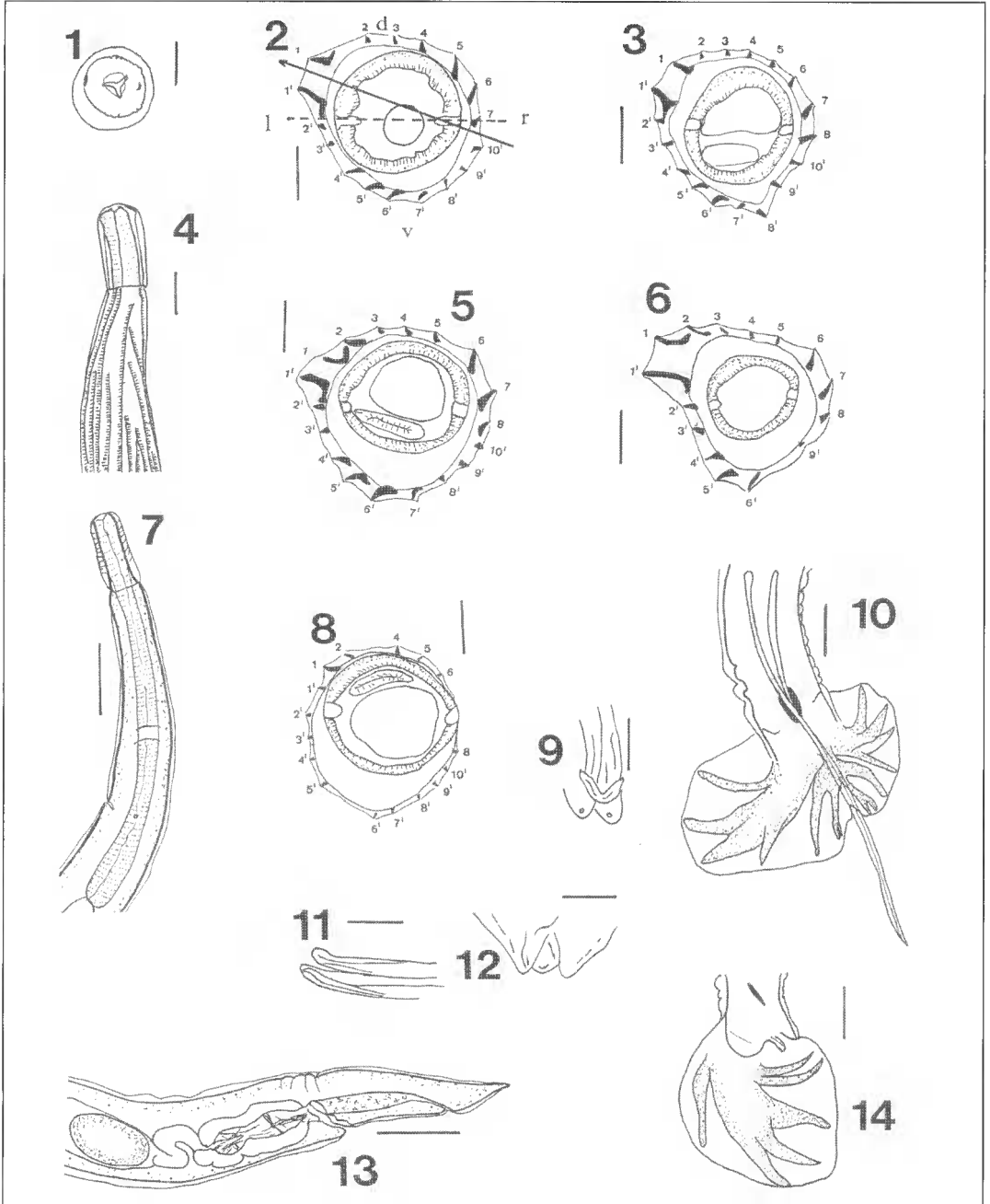
Rattus fuscipes, *R. lutreolus* (Gray) and *R. sordidus* (see Smales, 1997). Species of *Odilia* have also been found in the hydromyine *Mallomys rothschildi* Thomas from Irian Jaya, now Papua, Indonesia and the murines *Rattus xanthurus* Gray and *Maxomys musschenbroekii* Jentink from Sulawesi, Indonesia (Hasegawa & Sayaffrudin, 1994; 1995; Hasegawa *et al.*, 1999).

Rattus leucopus, the Cape York rat, and *R. sordidus*, the canefield rat, are both found in northern Queensland and the island of New Guinea, the only two endemic murines that are found on both sides of Torres Strait (Flannery, 1995). This distribution provides evidence of recent past land bridges, probably in the Pleistocene, between the two land masses (Moore & Leung, 1995). Observations on the host range of the species and the significance of the geographical distribution of the genus *Odilia*, given the geographical distributions of the hosts are presented.

Materials And Methods

The specimens from *R. leucopus* were fixed in 10% formalin, stored in 70% ethanol and examined in lactophenol. En face preparations and transverse sections were cut by hand using a cataract scalpel and mounted in polyvinyl lactophenol. Measurements of 10 males and 10 females from *Rattus leucopus* were taken using an ocular micrometer and given as the range followed by the mean in parentheses, in micrometres unless otherwise stated. Drawings were made with the aid of an Olympus BH Nomarski interference contrast microscope and drawing tube. Specimens are held in the CSIRO Wildlife collection, Canberra (CSIRO) and the South Australian Museum, Adelaide (SAM AHC). Terminology and classification used follows

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Figs. 1-14. *Odiha emanuelae* (Mawson, 1961). Female head, en face view. 2. Female, anterior body section through oesophageal region, arrow indicating axis of orientation of synlophe. 3. Male, mid body section. 4. Female, anterior end, lateral view showing origins of ridges of synlophe. 5. Female, mid body section. 6. Male, section within posterior third of body. 7. Female, anterior end, lateral view. 8. Female, section within posterior quarter of body. 9. Genital cone, right ventral view. 10. Bursa, dorsal view, flattened. 11. Spicule tips, lateral view. 12. Genital cone, right lateral view. 13. Female, posterior end, left lateral view. 14. Male, posterior end, right lateral view. Abbreviations d, dorsal; l, left; r, right; v, ventral. Scale bars: 1, 9, 11, 12, 10 μm ; 2, 3, 5, 6, 8, 20 μm ; 4, 10, 25 μm ; 7, 13, 14, 50 μm .

Durette-Desset (1971, 1973, 1983, 1985), Beveridge & Durette-Desset (1992) and Durette-Desset *et al.* (1994). Rodent classification follows Strahan (1995).

Odilia emanuelae (Mawson, 1961)
(Figs 1-14)

Heligmonoides emanuelae Mawson, 1961, pp 809-810, figs 30-34 table 4, from *Rattus conatus* (syn *R. sordidus*) and *R. assimilis* (syn *R. fuscipes*); Durette-Desset (1969) p 738, fig 4C.

Austrostrongylus emanuelae: (Mawson, 1961) Durette-Desset 1971 p 65.

Odilia emanuelae: : (Mawson, 1961) Durette-Desset 1973 p 517; Smales 1992 p 75.

Material examined

From *Rattus sordidus*: holotype male, allotype female, Innisfail, (17° 32' S, 146° 01' E) Queensland, SAM AHC 41332; from *Rattus leucopus*: 55 males, 81 females, East Mc Illwraith Range, Cape York Peninsula (13° 45' S, 143° 20' E), Queensland coll. P. Catling, I. Mason and P. Haycock, 9. xiii. 1990, 10. iii. 1990, CSIRO N3293, N3296, N3324, N3325, N3326, N3329; from *Melomys cervinipes* (Gould) 10 males, 10 females, D'Aguillar Range (27° 50' S, 152° 45' E), Queensland, 19. ii. 1963, SAM AHC 5805, coll. Aland and Stewart, 26.viii. 1993, SAM AHC 32190, 32191, 32192. Comparison of the measurements of specimens from *Rattus sordidus*, type host, and *R. leucopus* are given in Table 1.

Redescription

Small coiled nematodes; prominent cephalic vesicle present; buccal capsule vestigial. Mouth opening triangular with rudimentary lips, surrounded by four double papillae, each comprising a cephalic plus externo-labial papilla and two lateral amphids. Internal labial papillae not visible. Oesophagus claviform; nerve ring surrounds oesophagus at about mid level; excretory pore and digitiform deirids at same level, posterior to nerve ring.

Synlophe: Longitudinal cuticular ridges continuous, extend from posterior margin of cephalic vesicle to just anterior to bursa or vulva; 17 in anterior, 18 in mid body; axis of orientation from right ventral to left dorsal at approximately 75° to frontal axis; 7-8 in dorsal side, 9-10 in ventral side; ridges 1 and 1' largest, forming typical type A carene, ridges 2, 3 smaller than ridges 1, ridges 4-6 increasing in size, ridges 7-10 decreasing in size. Posterior region of body with 15 (male), 17 (female) ridges reduced in size; dorsal side with 7-8; ventral side with 7-10 ridges.

Male

Length 1.3-1.64 (1.50) mm, maximum width 54-67 (60). Cephalic vesicle 42-56 (50.6) long. Oesophagus 300-420 (345) long; excretory pore 231, 340 from anterior end. Bursa asymmetrical, right lobe larger (rays of right lobe more robust); deep dorsal cleft. Dorsal ray symmetrical divided at about half its length, each branch dividing again at distal tip; terminal divisions, rays 9, 10 symmetrical; rays 8 arising at same level, right ray 8 more robust than left.

TABLE 1. Measurements of *Odilia emanuelae*, in μm unless otherwise stated, from two host species; 10 males and 10 females from each. Data for *Rattus fuscipes* are from Mawson (1961).

Locality	<i>Rattus leucopus</i> East McIllwraith Range	<i>Rattus fuscipes</i> Innisfail
Male		
Length, mm	1.3-1.64	2.2-2.6
Width	54-67	-
Cephalic vesicle	42-56	50-60
Oesophagus length	300-420	240-270
Ant. end to excretory pore	230, 340	190-220
nerve ring	-	-
deirid	-	190-220
Spicules	245-270	250-330
Gubernaculum	17-22	-
Female		
Length, mm	1.8-2.6	2.1-3.1
Width	63-74	-
Cephalic vesicle	50-56	50-60
Oesophagus length	240-410	270-290
Ant. end to excretory pore	-	200-222
nerve ring	-	-
deirid	-	200-222
Tail	30-43	40-50
Eggs	50-63 x 27-34	60-80 x 40-50
Vulva to tail tip	87-119	105-130

Rays 4, 5, 6 with common stem, reaching margin of bursa; rays 4 and 5 robust curving anteriorly, rays 6 slender, curving posteriorly. Rays 2 and 3 with common stem, robust, diverge distally, curve posteriorly, reaching margin of bursa. Genital cone short, ventral lobe with unpaired papilla 0, lightly sclerotized; dorsal lip bifid, each lobe with single papilla 7. Spicules equal, filiform, tips pointed, 245-270 (253) long. Gubernaculum 17-22 (19.5) long.

Female

Length 1.8-2.6 (2.1) mm; maximum width 63-74 (67). Cephalic vesicle 49.5-56 (51.5) long; oesophagus 240-410 (320) long. Vulva opens 87-119 (94.5) from tail tip; posterior end may or may not be flexed at right angles just behind vulva. Monodelphic, ovejector with sphincter 30, 35, shorter than vestibule 50, 60, infundibulum, about same length as sphincter. Tail 29.5-43 (35) long. Eggs in utero 49.5-63 (56.5) by 26.5-34 (30).

Key to species of the genus *Odilia*

1. Synlophe with discontinuous ventral ridges.....
.....*O. mackerassae* (Mawson, 1961)
Synlophe with continuous ridges.....2
2. Synlophe with 18 or more ridges in mid body..3
Synlophe with fewer than 18 ridges in mid body
.....10
3. Synlophe with 18 ridges in mid body.....4
Synlophe with more than 18 ridges in mid body
.....5
4. Synlophe with fewer than 18 ridges posteriorly,
12-15 in males. Gubernaculum 17-22 long;
spicule tips taper to sharp point. Female tail
conical, rounded tip*O. emanuelae*
(Mawson, 1961)
Synlophe with more than 18 ridges posteriorly,
24 in males. Gubernaculum 30-40 long; spicule
tips joined distally surrounded by transparent
membrane. Female tail tapers sharply from vulva
to pointed tip.....*O. tasmaniensis*
Gibbons & Spratt, 1995
5. Synlophe with 19-20 ridges (male) in mid body,
ridges becoming tiny posteriorly. Gubernaculum
19-22 long; spicule: body length 1: 6.5. Female
tail 30; eggs 59-78 x 29-42.....*O. mamasaensis*
Hasegawa, Miyata & Syafruddin, 1999
Synlophe with more than 20 ridges (male) in mid
body.....6
6. Synlophe with 21 ridges (male) in mid body.
Gubernaculum 28 long; spicule: body length 1: 8
.....*O. mawsonae* (Durette-Dcsset, 1969)
Synlophe with more than 21 ridges in mid body
.....7
7. Synlophe with up to 35 ridges in mid body8
Synlophe with more than 35 ridges in mid body
.....9
8. Synlophe with 24-25 (male), 24-28 (female)
ridges in mid body, 23 (male) 13 (female) ridges
becoming minute posteriorly. Gubernaculum 32-
37; spicule: body length 1:4. Female tail conical,
pointed tip; eggs 72-80 x 35-43*O. maxomyos*
Hasegawa, Miyata & Syafruddin, 1999
Synlophe with 22-29 ridges (male), 24-35 ridges
(female) in mid body, 29 (male), 26 (female)
ridges posteriorly. Gubernaculum absent; spicule:
body length: 1:13. Female tail with prepuce; eggs
60-70 x 40*O. praeputialis*
Gibbons & Spratt, 1995
9. Synlophe with many (male), 36 (female), even
sized ridges in mid body. Gubernaculum 20 long;
spicule: body length ratio 1:8. Female tail twisted
into 1-2 coils in front of vulva.....
.....*O. polyrhabdote* (Mawson, 1961)
Synlophe with 40 (male), 48 (female) ridges in
mid body. Spicule tips with hair like projection
60 from distal end supporting fan-like alae;
spicule: body length 1:9. Female tail conical 60-
70 long with prepuce*O. uronyos*
(Mawson, 1961)
10. Synlophe with 17 ridges in mid body, 20 (male),
19 (female) posteriorly. Gubernaculum 50 long;
spicule: body length 1:14. Eggs 70-80 x 40-50
.....*O. bainaie* Beveridge & Durette-Dcsset, 1992
Synlophe with fewer than 17 ridges in mid body
.....11
11. Synlophe with 16 ridges (male) in mid body, 16
ridges smaller posteriorly. Spicule: body length
1:16. Female tail 50 long; eggs 69-77 x 35-45 ...
.....*O. mallomyos* Hasegawa & Syafruddin, 1994
Synlophe not as above12
12. Synlophe with 15 (male), 16 (female) ridges in
mid body13
Synlophe with less than 15 (male), 16 (female)
ridges in mid body14
13. Synlophe with 16-20 minute ridges posteriorly.
Gubernaculum 32-43 long; spicule: body length
1:7. Female cuticle inflated proximally to tail.....
.....*O. moatensis* Hasegawa & Syafruddin, 1999
Synlophe with 30 (male), 50 (female) small even
ridges posteriorly. Gubernaculum 51-62 long;
spicule: body length 1:8. Female cuticle not
inflated proximally to tail.....*O. sulawesiensis*
Hasegawa & Syafruddin, 1999
14. Synlophe with 14 (male), 15 (female) ridges in
mid body, 16 (female), smaller even ridges
posteriorly. Gubernaculum 30 long; spicule tips
pointed; spicule: body length 1: 9-1: 11. Female
tail conical, rounded tip 40-50 long
.....*O. melomyos* (Mawson, 1961)
Synlophe with 14 ridges (male) in mid body.
Gubernaculum 25 long; spicule tips expanding,
bifid; spicule: body length 1:9. Female tail
conical, pointed tip, flexed sharply back on itself
.....*O. brachybursa* (Mawson, 1961)

Although Hasegawa & Syafruddin (1995) noted *Odilia* sp. 1 and *Odilia* sp. 2 from *Rattus* cf. *morotaiensis* from Indonesia, insufficient morphological data were provided to allow inclusion of these two species in the key.

Discussion

The present study of *O. emanuelae* revealed slight variations in the morphology of the species as compared with the description of Mawson (1961), particularly in the range of measurements, with specimens from *R. leucopus* smaller than those from *R. sordidus*. The spicule tips were described as widened and alate by Mawson (1961). Gibbons & Spratt (1995), however, commented that they broadened then tapered to a sharp tip. Examination of the type male, as well as the specimens from *R. leucopus* in this study confirmed this latter form. The ridges of the synlophes were counted by Mawson (1961) as up to 20 in the mid body but given and figured as 18 by Durette-Desset (1969) for a female worm from *R. sordidus*, as is the case for specimens from *R. leucopus*. These minor morphometric differences may be due to host induced variation and are not sufficient to establish a separate species. Consequently the material from *R. leucopus* is assigned to *O. emanuelae*. The host range is accordingly expanded to include a third endemic *Rattus* species.

The only other host records for *O. emanuelae* are from *M. cervinipes*, specimens from a single host deposited in the SAM and specimens collected during an unpublished survey of the helminths of *M. cervinipes* and *R. fuscipes* from the D'Aguilar Ranges, south east Queensland (Aland¹) in which two of 12 *M. cervinipes* were reported as being infected with *O. emanuelae*. Re-examination of this material revealed specimens of *O. emanuelae* in a third host, making a total of 4 infected *M. cervinipes*, all from the D'Aguilar Ranges. *Odilia emanuelae* has not been reported in other surveys of the helminths from melomys, such as that of Mawson (1961) although she examined hosts from Innisfail, the type locality (Mawson, 1961; Smales, 1997). This suggests that *Rattus* species are the normal hosts and that infections found in *M. cervinipes* in

this study are an example of an occasional infection occurring where normal and alternative hosts are sympatric. The geographic distribution of *O. emanuelae* has been extended further north from the type locality into Cape York and south to south east Queensland.

Previous interpretations of the origins of the Trichostrongylina in Australian rodents have presumed that the genus *Odilia* arose in Australia, co-evolving with the rodent sub family Hydromyinae (see Durette-Desset, 1985); that is with the earliest of the rodent invaders commonly known as the old endemics. The rodents are thought to have arrived in Australia some 5-10 million years ago (Watts & Aslin, 1981; Flannery, 1995). *Odilia* was then captured by more recent rodent arrivals, the Murinae new endemic *Rattus* species that crossed to Australia from New Guinea less than one million years ago (Smales, 1992; Beveridge & Durette-Desset, 1992; Gibbons & Spratt, 1995).

More recently, however *Odilia* species have been described from several Indonesian islands and occurring in both old endemic and new endemic hosts (Hasegawa & Syafruddin 1994; 1995; Hasegawa *et al.*, 1999). At the same time, new fossil evidence from Australia suggests more complex evolutionary processes than had first been thought. There is now evidence for at least three phases of immigration, both direct from Southeast Asia, and through New Guinea, involving both old and new endemics (Godthelp, 2001).

This new evidence suggests that ancestral forms of *Odilia* may have co-evolved with rodent hosts in Southeast Asia. The present host and geographic distribution therefore reflects a complex series of evolutionary events involving host switching and co-evolution as rodent faunas and their helminth communities migrate, and undergo evolutionary radiations. The more data gathered about rodent hosts and their parasites from Southeast Asia and Australasia the more complex the patterns of their relationships become.

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¹ Aland, K. (1993) BSc Hons Thesis, Dept of Parasitology, University of Queensland.

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